



Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*

Lawrence B. Martin^{a*}, Anthony J. Olejniczak^b, Mary C. Maas^c

^aDepartments of Anthropology and Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794-4364, USA

^bInterdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY 11794, USA

^cDepartment of Anthropology and Laboratory of Vertebrate Paleontology, the University of Texas, Austin, TX 78712, USA

Received 27 May 2003; accepted 25 August 2003

Abstract

Many living primates that feed on hard food have been observed to have thick-enameled molars. Among platyrrhine primates, members of the tribe Pitheciini (*Cacajao*, *Chiropotes*, and *Pithecia*) are the most specialized seed and nut predators, and *Cebus apella* also includes exceptionally hard foods in its diet. To examine the hypothesized relationship between thick enamel and hard-object feeding, we sectioned small samples of molars from the platyrrhine primates *Aotus trivergatus*, *Ateles paniscus*, *Callicebus moloch*, *Cebus apella*, *Cacajao calvus*, *Chiropotes satanas*, *Pithecia monachus*, and *Pithecia pithecia*. We measured relative enamel thickness and examined enamel microstructure, paying special attention to the development of prism decussation and its optical manifestation, Hunter-Schreger Bands (HSB). *Cebus apella* has thick enamel with well-defined but sinuous HSB overlain by a substantial layer of radial prisms. *Aotus* and *Callicebus* have thin enamel consisting primarily of radial enamel with no HSB, *Ateles* has thin enamel with moderately developed HSB and an outer layer of radial prisms, and the thin enamel of the pitheciins (*Cacajao*, *Chiropotes*, and *Pithecia*) has extremely well-defined HSB. Among platyrrhines, two groups that feed on hard objects process these hard foods in different ways. *Cebus apella* masticates hard and brittle seeds with its thick-enameled cheek teeth. Pitheciin sclerocarpic foragers open hard husks with their canines but chew relatively soft and pliable seeds with their molars. These results reveal that thick enamel per se is not a prerequisite for hard object feeding. The Miocene hominoid *Kenyapithecus* may have included hard objects in its diet, but its thick-enameled molars indicate that its feeding adaptations differed from those of the pitheciins. The morphology of both the anterior and posterior dentition, including enamel thickness and microstructure, should be taken into consideration when inferring the dietary regime of fossil species.

© 2003 Elsevier Ltd. All rights reserved.

Keywords: Pitheciini; Enamel thickness; Nut-cracking; Seed-eating; Hunter-Schreger bands; Enamel microstructure; Tooth function; Sclerocarpic foraging; *Kenyapithecus*

* Corresponding author. Tel.: +1-631-632-7625; fax: +1-631-632-9165

E-mail addresses: lawrence.martin@stonybrook.edu (L.B. Martin), anthony.olejniczak@stonybrook.edu (A.J. Olejniczak), mcaas@prodigy.net.mx (M.C. Maas).

This article is dedicated to the memory of our friend and colleague Warren G. Kinzey, with whom we began this study.

Introduction

Enamel thickness has long been of interest to students of primate evolution and adaptation. The emphasis of many studies, however, has been on the phylogenetic significance of changes in relative enamel thickness, rather than on the function of thick enamel. Two studies in particular have incorporated functional hypotheses in scenarios relevant to the increase in enamel thickness seen in the evolution of the Hominoidea. Jolly (1970) proposed a seed-eating hypothesis in which he suggested that adaptations to a diet of seeds could explain many of the features associated with hominization. This adaptation was seen as evolving in a terrestrial primate occupying an open country environment. Kay (1981) proposed that a nut-cracking hypothesis was a more suitable model to explain the evolution of thick enamel. He provided metric data on enamel thickness in a variety of anthropoid primates, based on measurements of naturally exposed enamel in wear facets on lower molars. Contrary to Jolly's seed-eating hypothesis, Kay (1981) showed that thick enamel could be found in animals that were neither terrestrial nor associated with an open country environment, but instead in animals that fed on hard objects such as seeds.

Comparative studies of primates and other mammals suggest that the microstructure of tooth enamel, as well as its thickness, plays a role in hard-object feeding adaptations. Primate tooth enamel, like that of other mammals, consists of different combinations of three organizational types: prismless enamel, radial prismatic enamel, and decussating prismatic enamel (e.g., Maas and Dumont, 1999; Martin et al., 1988). Radial prisms extend straight from the enamel dentine junction to the outer tooth surface. Prism decussation describes the alternating orientations of enamel prisms in adjacent horizontal layers of enamel and is thought to enhance resistance to crack propagation in the enamel of animals whose teeth are subject to high stress (Pfretzschner, 1986; von

Koenigswald et al., 1987; Rensberger, 1993). It is common in primates to find bands of prisms that form zones that have different orientations and which have been described as Hunter-Schreger bands (HSB). Hunter-Schreger bands result from the different orientations of zones of prisms rather than the crossing over of adjacent layers of prisms (as would be seen in certain rodents) so their formation is a special case of prism decussation. Radial prisms, because their orientation is perpendicular to the tooth surface, are more resistant to abrasive wear than decussating prisms, but are less resistant to crack propagation (Maas and Dumont, 1999). In most primates, prismless enamel is restricted to a relatively thin layer on the surface of the tooth and is thought to be less resistant to crack propagation than decussating enamel. Thus, the bulk of the enamel thickness consists of radial prismatic enamel, decussating prismatic enamel, or a combination of these two types. If present, HSB may be poorly developed (gradual, ill-defined zone boundaries and an irregular distribution) or may be strongly expressed (abrupt boundaries between zones of differently oriented prisms and zones closely spaced and regularly distributed). The relative proportions of enamel types and the development of the HSB influence the physical properties of primate enamel, and thus the resistance of teeth to fracture and wear (Maas and Dumont, 1999).

The platyrrhine primates belonging to the tribe Pitheciini (the saki-uakaris: *Cacajao*, *Chiropotes*, and *Pithecia*) are among the most specialized primate seed and nut predators and dispersers (Norconk et al., 1998; Boubli, 1999). The pitheciin fossil record (e.g., *Propithecium neuquensis*, *Nuciraptor rubicae*) indicates that the lineage began to exploit a hard-object feeding niche by the middle Miocene (Meldrum and Kay, 1997; Kay et al., 1998). Extant pitheciins are found in lowland and highland forests of the Amazon and Orinoco basins. *Chiropotes* and *Pithecia* frequently occur sympatrically and are usually found in non-flooded forests, whereas *Cacajao* is found in flooded forests (*C. calvus*) or non-flooded forests (*C. melanocephalus*) (Boubli and Ditchfield, 2000).

The most significant food item consumed by all three pitheciin genera is seeds. In times of resource

stress, *Pithecia*, *Chiropotes*, and *Cacajao* all increase consumption of seeds. *Cacajao* does so except during a brief interval when virtually all fruit is absent from the trees, during which time they forage for newly germinating seeds on the ground; this is made possible by the absence of large terrestrial frugivorous competitors in the *várzea* (Ayres, 1989). All three extant pitheciin genera are predispersal seed predators (Janzen, 1971), eat fruit predominantly that are covered with a hard pericarp, and are thus sclerocarpic foragers (Kinzey and Norconk, 1990). Sclerocarpic foraging is characterized by the mastication of relatively soft seeds by the posterior dentition after a fruit's hard pericarp has been opened with the anterior dentition (Kinzey and Norconk, 1990). This is in contrast to the relatively hard seeds and nuts eaten by other primates (e.g., *Cebus apella*). It is likely that different types of seeds require different molar adaptations for effective mastication.

In this study, we investigate the nature of molar enamel thickness and microstructure in extant pitheciin sclerocarpic foragers and a small sample of other platyrrhine primates. The middle Miocene fossil hominoid *Kenyapithecus* has been described as a sclerocarpic forager because aspects of its dental and gnathic morphology appear to be analogous to the pitheciin condition (McCrossin and Benefit, 1997). Molar microstructure and enamel thickness in *Kenyapithecus* are compared to the platyrrhine sample in order to explore this hypothesis.

Materials and methods

We sectioned a sample of platyrrhine molar teeth to measure relative enamel thickness in controlled planes of section and to document enamel microstructure. The sample includes unworn or lightly worn molars extracted from skulls of *Aotus trivergatus*, *Ateles paniscus*, *Cacajao calvus*, *Callicebus moloch*, *Cebus apella*, *Chiropotes satanas*, and *Pithecia monachus* (Table 1). The extracted teeth were refluxed in a mixture of chloroform and methanol and embedded in methyl methacrylate, following procedures outlined by Boyde and Tamarin (1984) and Boyde (1989).

The teeth were sectioned through the mesial cusps in a coronal plane using a tungsten wire saw (Unipress). A 40 μm wire was used, allowing the tooth to be cut with the loss of approximately 50 μm of tissue. Following the first cut, the specimen was advanced 150 μm and a second cut was made to remove a thin section for use in a parallel study employing polarized light microscopy. As a result, the two block faces on which enamel thickness measurements were taken in the present study are approximately 200 μm apart. The sections were polished with a series of diamond pastes (6 μm , 1 μm , 0.25 μm) on a grinder-polisher (Buehler), etched with 0.5% H_3PO_4 for 60 seconds, and sputter-coated with silver for examination with an Amray 1810 scanning electron microscope. Overview micrographs were recorded of the entire section at working distances between 12 and 16 mm in order to produce accurate measurements. Images were recorded on Polaroid 55 film. A representative overview of a molar cross-section from each of the genera examined in this study is provided in Fig. 1.

Enamel thickness measurements were recorded from 8×10 inch prints using a digitizing tablet with SigmaScan software (Jandel Scientific). The magnification of the micrographs was calibrated by field width, field height, and field area calculated from the magnification at which the image was recorded. This is a more precise method than using the micrograph's scale bar because it maximizes the reference distance to be measured, and thus minimizes errors in calibration. It also has the advantage that all images are calibrated using the same reference distance so that any error in entering the calibration should be constant. If the accuracy of digitizing is 0.1 mm, this is a very small fraction of the field width or area. The micron bar on the micrograph may range from only 10 to 100 μm in size and thus the recording error will always be a greater proportion of the distance measured, and will also vary from one micrograph to another depending on the magnification at which the image was recorded.

The measurements recorded include areas and perimeter lengths (Fig. 2). Each measurement was repeated three times on each specimen and the values were averaged to reduce the effect of

Table 1

Enamel thickness measurements (b, c, e) and relative enamel thickness (RET) for each specimen in this study, and genus averages^a

Taxon	Specimen	Tooth	b (mm ²)	c (mm ²)	e (mm)	RET
<i>Aotus</i>	USNM 396976	M ¹	3.58	1.23	6.38	10.19
<i>Aotus</i>	USNM 396780	M ²	2.91	1.15	5.21	12.94
<i>Aotus</i>	USNM 396971	M ₁	2.98	1.08	5.19	12.05
Mean			3.16	1.15	5.59	11.73
<i>Ateles</i>	RM 16176-28	M ²	9.65	2.89	10.70	8.69
<i>Ateles</i>	RM 16124-29	M ³	4.36	1.29	6.57	9.40
<i>Ateles</i>	RM 16176-19	M ³	6.53	2.40	8.88	10.58
<i>Ateles</i>	RM 16176-27	M ¹	9.85	2.39	11.08	6.87
Mean			7.60	2.24	9.31	8.89
<i>Cacajao</i>	JGF NCj1-28	M ²	8.74	3.11	8.81	11.94
<i>Cacajao</i>	JGF NCj1-38	M ₂	8.06	2.42	8.66	9.84
<i>Cacajao</i>	JGF NCj1-29	M ³	5.05	1.90	6.59	12.83
Mean			7.28	2.48	8.02	11.54
<i>Callicebus</i>	USNM 541410	M ₂	4.41	1.65	6.38	12.32
<i>Cebus</i>	AMNH 100138	M ₁	6.70	3.97	7.94	19.32
<i>Cebus</i>	AMNH 17345	M ₁	7.37	4.07	8.16	18.37
Mean			7.04	4.02	8.05	18.84
<i>Chiropotes</i>	RM 16208-18	M ²	8.52	1.91	8.26	7.92
<i>Chiropotes</i>	RM 16160-48	M ₂	4.30	1.40	6.19	10.91
<i>Chiropotes</i>	RM 16160-38	M ₂	5.03	1.49	6.78	9.80
Mean			5.95	1.60	7.08	9.54
<i>Pithecia</i>	USNM 397312	M ¹	5.85	2.05	7.43	11.41
<i>Pithecia</i>	USNM 307403	M ₁	5.47	1.95	7.06	11.81
Mean			5.66	2.00	7.25	11.61

^aUSNM—Department of Mammalogy, Smithsonian Institution National Museum of Natural History; RM and JGF—Department of Anatomical Sciences at Stony Brook University; AMNH—the American Museum of Natural History.

measurement error. Differences among the three values were minimal. A number of linear enamel thickness measurements corresponding to those reported elsewhere for other taxa (Martin, 1983; Grine and Martin, 1988; Macho and Berner, 1993, 1994; Ulhaas et al., 1999; Schwartz, 2000) were not included in our analysis, but they are provided in Appendix A, and are named following Martin (1983).

Oblique sections through teeth increase the apparent enamel thickness. Martin (1983, 1985) showed that the section in which the exposed enamel thickness corresponds most closely to the true (radial) enamel thickness is the one in which the enamel measurements are at a minimum and the dentine measurements are at a maximum. Thus, in this study, both available faces were

measured for each tooth (with the exception of one specimen for which one face was not measurable) and the values recorded for the plane with the minimum enamel measurements and maximum dentine measurements.

Martin (1983, 1985) argued that the ideal measurement of the amount of enamel on a tooth would be its volume. Volume could be converted to a linear dimension by dividing it by the area of the enamel-dentine junction, yielding an average enamel thickness that is effectively equivalent to the average straight-line distance traveled by an ameloblast (enamel-secreting cell) from the enamel-dentine junction to the enamel surface during its secretory life. This value may be approximated in a planar section by dividing the area of the enamel cap (Fig. 2 c) by the length of the

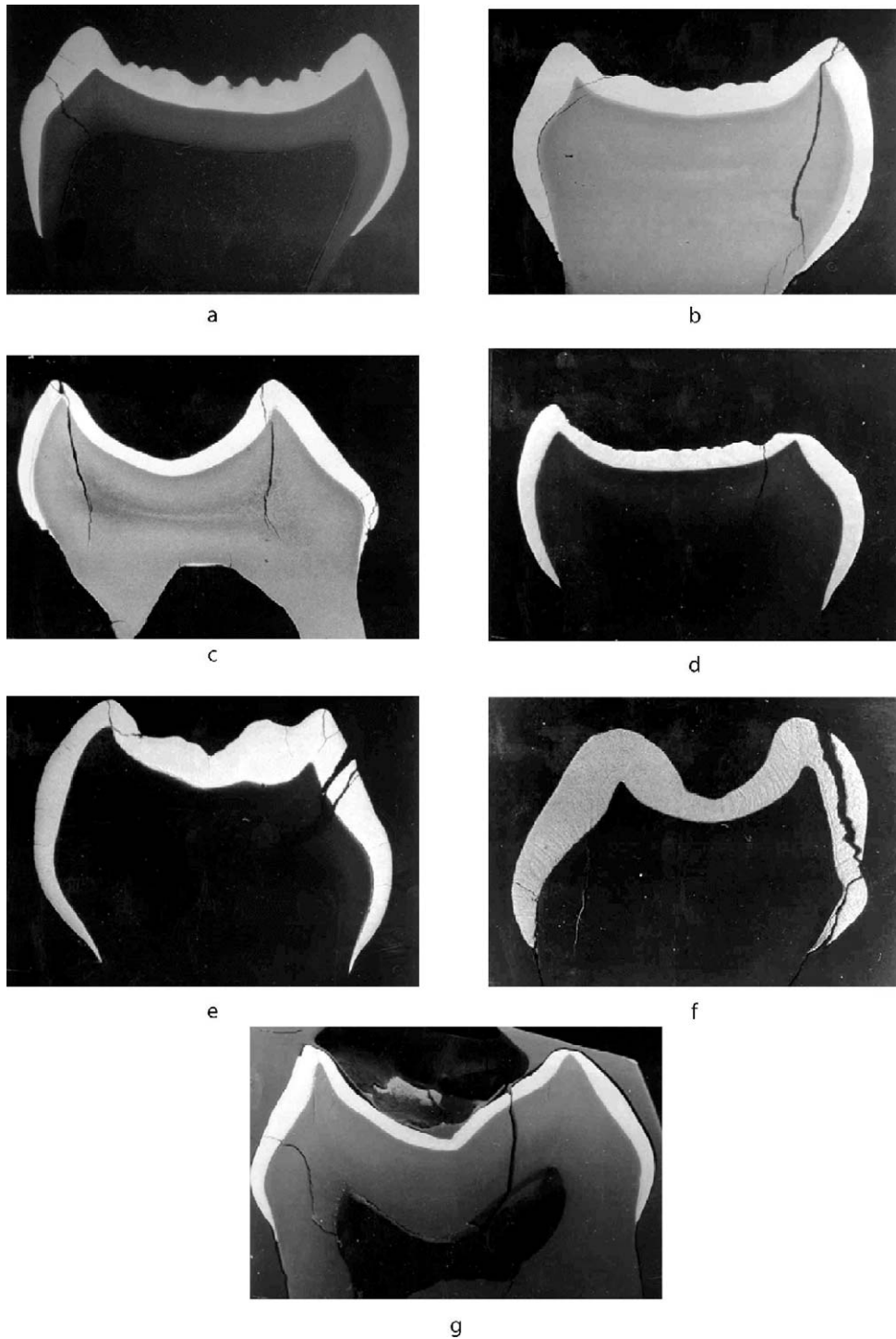


Fig. 1. Representative overview images of the teeth used in this study (not to scale). a, *Pithecia*; b, *Chiropotes*; c, *Aotus*; d, *Cacajao*; e, *Callicebus*; f, *Cebus*; g, *Ateles*.

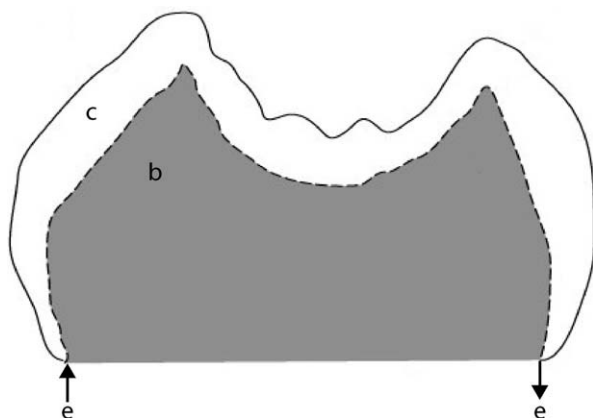


Fig. 2. Measurements recorded in this study. c, the cross-sectional area of the enamel cap; b, the cross-sectional area of dentine; e, the length of the enamel-dentine junction.

enamel-dentine junction (Fig. 2 e), which gives an average enamel thickness and is the best overall summary of enamel thickness for the entire crown.

Absolute values of enamel thickness have little value when comparing animals of different sizes. Martin (1983, 1985) developed several indices of relative enamel thickness that scaled the enamel thickness to the size of the tooth. None of the scaling parameters included any enamel in their magnitude (i.e., not crown length, breadth, or area) as these are not independent variables. Martin found that, among hominoids, the best scaling factor for relative enamel thickness calculations was the square root of dentine area (Fig. 2 b). Dumont's study of enamel thickness in chiropterans and primates (including some platyrrhines) did not find a significant tendency for relative enamel thickness ($c/e \div \sqrt{b}$) to increase with body size and tooth size, and Shellis et al. (1998) report that dentine area scales isometrically with body size across a wide range of primates. This confirms that Martin's relative index based on dentine area is a suitable choice for comparing primate species, and so it is used in this study to eliminate the effects of body size in interspecies comparisons.

Rensberger (1993) developed a protocol for quantifying the relative prevalence of Hunter-Schreger bands within a tooth, but his method is difficult to apply because of inconsistencies be-

tween different forms of microscopy and because patterns of decussation (and therefore definition of HSB) vary considerably across species. For example, polarized light microscopy blurs the boundary between adjacent decussation zones, making demarcation of individual Hunter-Schreger bands somewhat subjective. While scanning electron microscopy shows individual prism boundaries, zones are still difficult to quantify because of the irregular and often gradual change in prism orientation in boundaries between decussation zones. Further complicating attempts to quantify HSB, in many primates the decussation patterns differ within a single tooth, including cusp tips, basins, and near the root-crown junction. Finally, most primate enamel consists of a "schmelzmuster" (von Koenigswald and Clemens, 1992) of several enamel types (prismless enamel, radial enamel, and HSB), and variation in the schmelzmuster must also be taken into account when evaluating the mechanical properties of a tooth and comparing enamel in different species.

As a result, our qualitative assessment of enamel types for each taxon includes 1) presence or absence, and approximate proportions, of HSB, radial enamel, and prismless enamel and 2) descriptive characteristics of HSB, including regularity of spacing, width, and their course from the enamel-dentine junction (sinusoidal or straight; in sectioned teeth a sinusoidal course reflects the vertical undulation of prism decussation zones from the EDJ to the surface, and a straight course reflects lack of undulation in a vertical plane). The assessment of HSB is based on Rensberger's criteria for whether enamel decussation is an effective crack inhibitor.

Results

The average values for enamel thickness measurements and the relative enamel thickness index for each specimen, and the genus averages, are given in Table 1. *Cebus apella* has remarkably thick enamel compared to the rest of the sample. Dixon's test for outliers (Sokal and Rohlf, 1995) confirms that *Cebus apella* is a statistical outlier ($r_{10}=0.61$, $\alpha=0.05$) compared to the rest of the

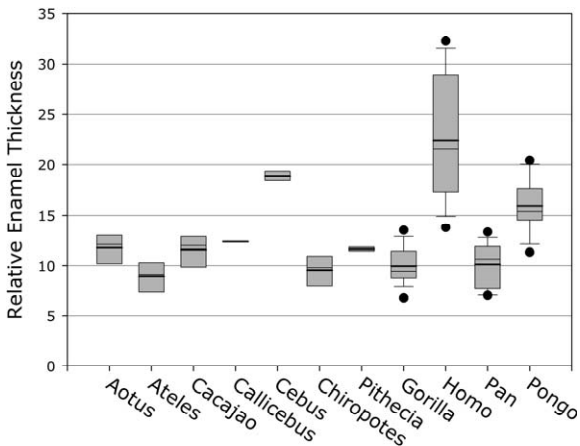


Fig. 3. Boxplot displaying the relative enamel thickness values of the platyrrhine genera examined in this study and the extant hominoids reported by Martin (1983, 1985). Ends of boxes represent 25th and 75th percentiles; whiskers represent 10th and 90th percentiles; thick line in box represent mean; thin line in box represents median; points represent outliers.

platyrrhine taxa. The other taxa have either thin (8.90–11.3) or intermediate-thin (11.30–14.65) enamel, following the categories defined by Martin (1983). Fig. 3 depicts the relative enamel thicknesses of the platyrrhine genera examined in this study, in the context of the hominoids measured by Martin (1983).

Martin's categories were based on 95% confidence intervals obtained from his sample of extant hominoid molars. In light of recent studies that quantified enamel thickness in other primate groups and non-primate mammals (Appendix B), these categories must be refined. The very thin enamel of the chiropteran *Eumops*, for instance, falls below the lower bound of Martin's "thin" category; if there were a "hyper-thin" category based on the same 95% confidence intervals, it would still not accommodate *Eumops*. Appendix B catalogues the published enamel thickness values of all of the extant taxa that have been measured in the same plane of section used in this study. Fig. 4 demonstrates that the few non-primate mammals sampled have relatively thin enamel compared to primates. Strepsirrhines generally have thicker enamel than the non-primates; platyrrhine enamel is thicker than strepsirrhine enamel on average, and catarrhines have the thickest molar enamel. It

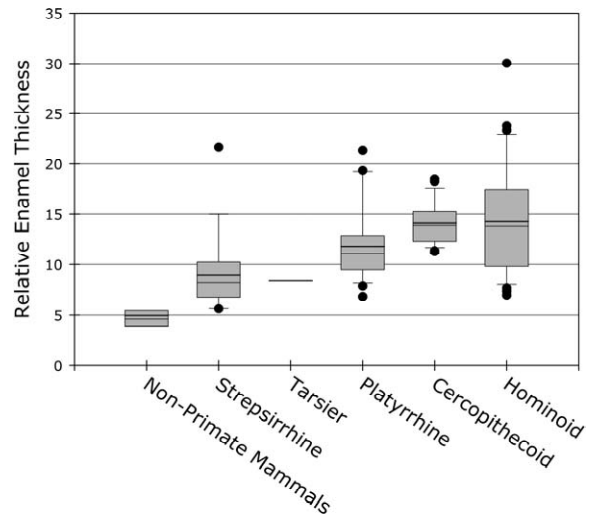


Fig. 4. Boxplot displaying published relative enamel thickness values in extant primate radiations and some non-primate mammals. The thick-enamelled outlier among strepsirrhines is *Daubentonia madagascarensis*; the thick-enamelled end of the platyrrhine distribution is *Cebus apella*; the thick-enamelled outliers among Hominoidea are *Homo sapiens*. Non-primate mammals include *Tupaia tana* (Scandentia), *Eumops perotis*, *E. underwoodi*, *Hipposideros caffer*, *H. commersoni*, *Myotis lucifugus*, and *M. velifer* (Chiroptera). Ends of boxes represent 25th and 75th percentiles; whiskers represent 10th and 90th percentiles; thick line in box represent mean; thin line in box represents median; points represent outliers. See Appendix B for publications from which the data were obtained.

is in this broad context that the "thin" enamel of the platyrrhines must be interpreted—their enamel is thin when compared to many catarrhines, but it is categorically thicker than the enamel of many strepsirrhines, *Tarsius*, and those non-primate mammals that have been sampled.

Our results are in general agreement with other studies that report relative enamel thickness values for platyrrhines. Dumont (1995) found that *Cebus apella* ($n=1$) has a relative enamel thickness of 21.36. Measurements reported by Shellis et al. (1998): table 2 for *C. apella* ($n=1$) yield a relative enamel thickness of 19.22. The average value presented here for *C. apella* is of similar magnitude (18.84, $n=2$). Shellis et al.'s (table 4) measurements of a single *Ateles* molar yield a relative enamel thickness of 13.07. Our sample of four *Ateles paniscus* molars yielded an average relative enamel thickness of 8.89. This difference might be due to

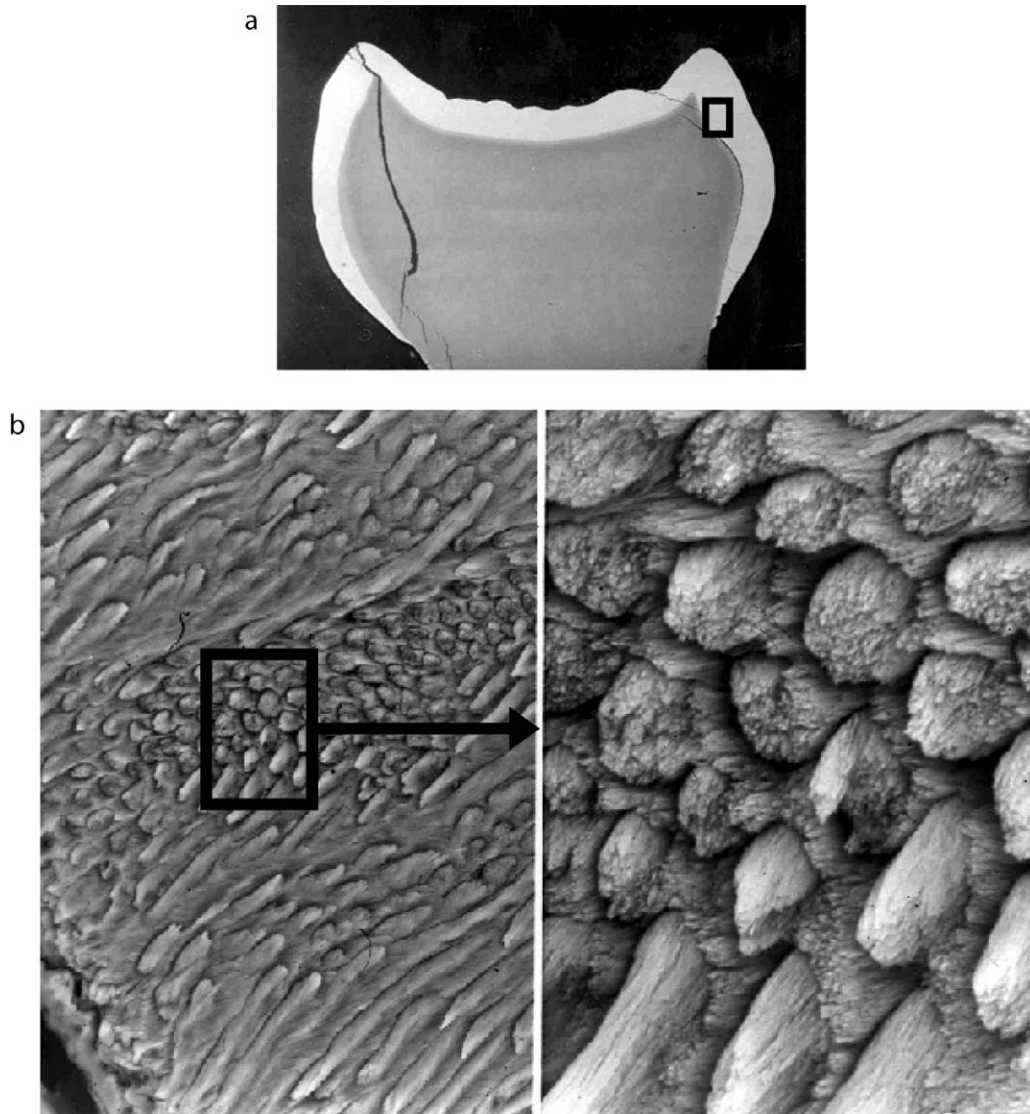


Fig. 5. Decussation in a *Chiropotes* molar. The box in Fig. 5a has been enlarged in Fig. 5b (left), in order to demonstrate alternating bands of enamel prisms (parazonal and diazonal, or Hunter-Schreger bands). The right side of Fig. 5b is an enlargement of a diazone, in which the ends of enamel prisms are seen.

interspecific variation (Shellis et al.'s *Ateles* molar was of unknown species affiliation), but given the small sample sizes in both studies, the variation may also be due to sampling error.

All of the pitheciins examined have HSB that extend from close to the enamel-dentine junction almost to the outer surface of the tooth. All have a thin layer of prismless enamel at the surface, but

radial enamel is either absent or only a thin layer (less than 10% of the enamel thickness). The HSB boundaries are clearly defined, and have a straight course from the EDJ to the tooth surface, without apparent vertical undulation. Fig. 5 shows decussation in a *Chiropotes* molar, demonstrating that the HSB are well-defined and extend almost to the enamel surface. In *Cebus* and *Ateles*, HSB extend

from the EDJ approximately to the outer third of the enamel, and are overlain by a layer of radial prisms that is always thicker than that in the pitheciins. As in pitheciins, there is a very thin outermost layer of prismless enamel. The HSB boundaries are clearly defined in both *Ateles* and *Cebus*, but, in contrast to the pitheciins, there appears to be a wider transitional zone, representing a gradual change in prism orientation between adjacent zones. The sinuous appearance of the bands in these longitudinal sections (especially in *Cebus apella*) indicates that there is some vertical undulation of decussation zones. *Aotus* and *Callicebus* have no Hunter-Schreger bands; the bulk of the enamel thickness in these specimens consists of radial enamel overlain by a thin outer layer of prismless enamel. Fig. 6 demonstrates the variability of HSB development in the sample examined in this study.

Discussion

Pitheciin adaptations to sclerocarpic foraging

The ability of pitheciins to open the hard pericarp of fruit in order to obtain nutritious seeds is a critical function of their anterior dentition (Rosenberger and Kinzey, 1976). Kinzey and Norconk (1990) have referred to this adaptation as sclerocarpic foraging. Fruits with puncture resistances up to 38 kg/mm² and 6.8 kg/mm² have been opened by *Chiropotes Satanas* and *Pithecia pithecia*, respectively (Kinzey and Norconk, 1990). Both species eat fruit that is considerably harder on average than the hardest fruit eaten by spider monkeys (maximum=1.4 kg/mm²), which are sympatric with *Chiropotes*. Quantitative field data are not available for *Cacajao*, but Ayres (1986) reported that *Cacajao calvus* opened hard shells of immature fruit to obtain seeds and that the most preferred seeds were from fruit with hard husks. According to Barnett and da Cunha (1991), golden-backed uakaris (*C. melanocephalus*) were seen feeding predominantly on fruit with hard husks. In a survey on the Rio Negro, Lehman and Robertson (1994) observed that *C. melanocephalus* ate immature seeds of

Manilkara fruit (Sapotaceae), which have a thick, hard husk.

Derived features of the pitheciin anterior dentition include characters of both the incisor and the canine, but the most remarkable shared features are the enormous, laterally splayed canines, used in puncturing the pericarp of hard fruit. The canines are of greater height and caliber than is expected relative to body size and relative to the length of the postcanine dentition (Orlosky, 1973; Rosenberger, 1979; Anapol and Lee, 1994). The lack of sexual dimorphism in pitheciin dental morphology (Swindler, 1976; Hershkovitz, 1985) suggests that the robust canine is associated with feeding and not with social behavior. The canine teeth, unlike those of other platyrrhines, are buccolingually tapered (Hershkovitz, 1985). This produces a wedge-like morphology with well-developed cutting edges on the mesial and distal surfaces of both the upper and lower canines. The canine is functionally separated from the incisors in two ways: first, in both jaws a diastema isolates the canine from the lateral incisor; second, the orientation of the canine cutting edges differs from that of all other ceboids in that they are rotated medially, and thus are positioned outside the contour of the dental arcade. This frees the canines from interfering with the incisors when they are used to puncture large food items, and also facilitates puncturing a hard object with considerable force (Anapol and Lee, 1994).

In contrast to the pericarp, the seeds of fruits eaten by *Pithecia* and *Chiropotes* are less puncture resistant. The average resistance of seeds crushed by *Pithecia* was 10.8 ± 0.8 kg/mm² and the average for *Chiropotes* was only 7.2 ± 0.7 kg/mm² (Kinzey, 1992). Among species of fruit whose seeds were masticated by *Pithecia* and *Chiropotes*, the maximum crushing resistance of whole seeds was 37 kg/mm². They are much softer, for example, than seeds swallowed (without mastication) by *Ateles* (Kinzey and Norconk, 1990), which have a maximum crushing resistance of 148 kg/mm². The fact that these softer seeds are processed largely by the posterior dentition, whereas the hard pericarp is processed by the robust anterior dentition may account for the distinctive features of the pitheciin postcanine teeth, including their thin enamel.

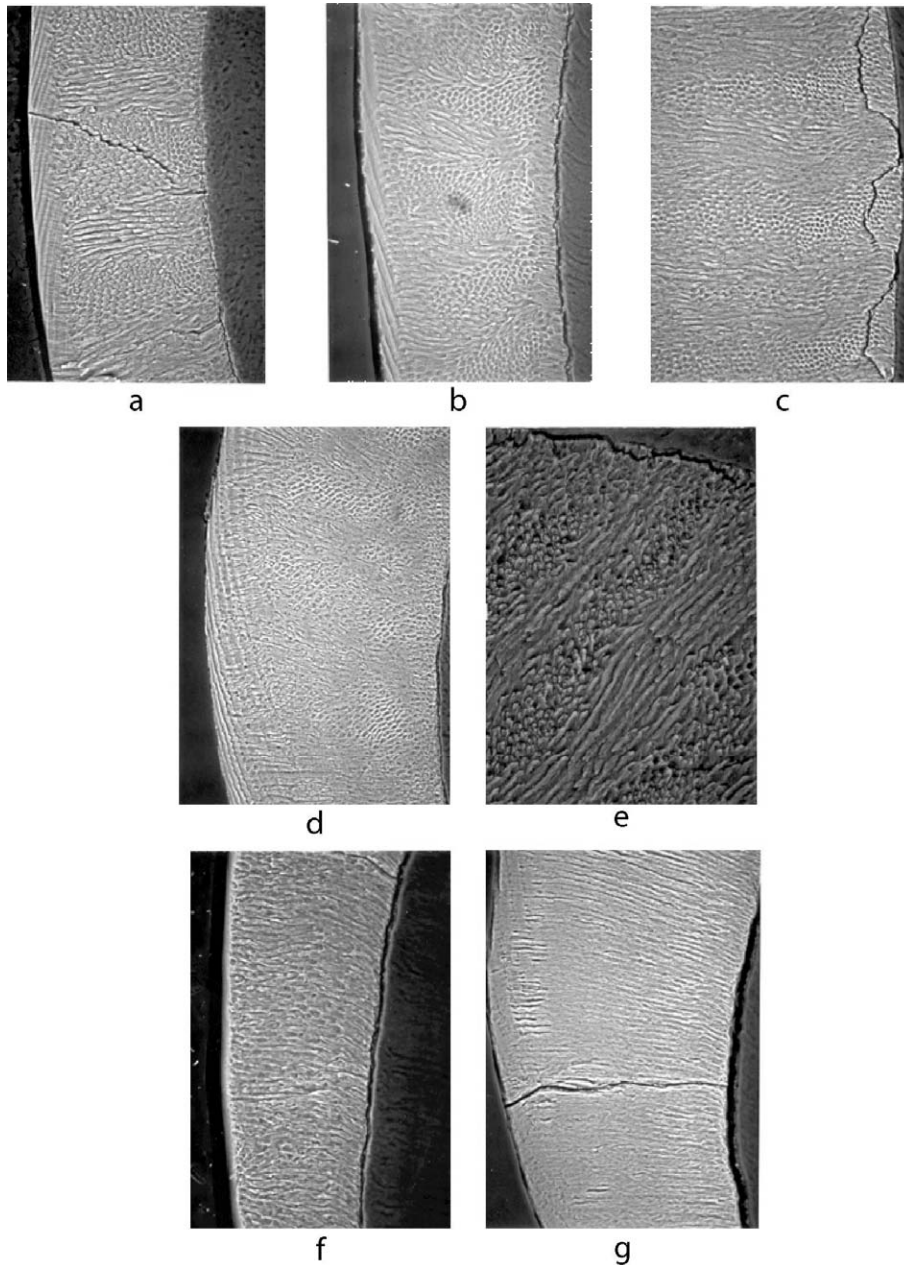


Fig. 6. Scanning electron micrographs demonstrating variability in Hunter-Schreger band development (not to scale). EDJ is to right, enamel surface is to the left (except in Fig. 6e, where the EDJ is to the top). a, *Cacajao*; b, *Chiropotes*; c, *Pithecia*; d, *Ateles*; e, *Cebus*; f, *Aotus*; g, *Callicebus*. *Cacajao*, *Chiropotes*, and *Pithecia* have well-developed Hunter-Schreger bands; *Ateles* and *Cebus* have moderately developed bands; *Aotus* and *Callicebus* do not have Hunter-Schreger bands.

In light of the relationship between seed and nut eating and thick enamel described by Jolly (1970) and Kay (1981), the thin enamel reported for all of

the pitheciins is unexpected. The posterior dentition of pitheciins is morphologically specialized for the mastication of tough, pliable, and generally

soft seeds, rather than hard food items. These specializations include enlarged, molariform upper and lower P4, both of which have crenulated basins in many individuals. Additionally, the low occlusal relief and presence of enamel crenulations on all upper and lower molars is one of the hallmarks of the pitheciins. Although it has been suggested that this specialized molar morphology (in *Cacajao*, Ayres [1989]; in *Chiropotes*, van Roosmalen et al. [1988]) is related to chewing hard food items, Rosenberger and Kinzey (1976) argued that, by analogy with phyllostomid bats, the low occlusal relief is related to chewing relatively soft food. Field evidence of feeding in both *Chiropotes satanas* (Kinzey and Norconk, 1990) and *Pithecia pithecia* (Kinzey and Norconk, 1993) suggests that after opening fruit with hard husks using robust canines, pitheciins do, in fact, masticate tough, but relatively soft and pliable seeds. This would also explain their lack of thick molar enamel, predicted by Jolly (1970) and Kay (1981) for primate seed and nut eaters.

It has been convincingly shown that HSB are a crack-stopping mechanism (von Koenigswald et al., 1987; Rensberger, 1993). If pitheciins masticate relatively soft, pliable seeds with their molars, and if HSB development is for the purpose of preventing the propagation of cracks in the enamel due to hard object mastication, then their strong molar prism decussation is unexpected and warrants explanation. von Koenigswald et al. (1987) documented the occurrence of HSB in a variety of extant and fossil mammals with molar widths greater than 3 mm, which in primates equates to a body size of about 1500–2000 g (Maas and Dumont, 1999). They hypothesized that herbivorous mammals of this size or larger produce normal chewing forces of sufficient magnitude to fracture enamel, absent the crack-stopping mechanism provided by prism decussation. A comparative survey supports the association between body size and prism decussation in primates, with the intriguing exception of some callithrichines (Maas and Dumont, 1999). Pitheciins all fall above the body-size threshold for HSB, and therefore would be expected to have decussating prisms organized in zones.

However, the distinct, well-defined boundaries of pitheciin HSB, the lack of transitional zones

between HSB, and their straight course and extension throughout almost the entire thickness of the enamel are all consistent with Rensberger's (Rensberger, 1993) criteria for strong decussation, and indicate that pitheciin teeth are structurally extremely resistant to crack propagation, despite their thin enamel. This suggests the possibility that some factor in addition to body size has influenced the enamel architecture of pitheciins. It is unknown whether the pitheciins have highly decussated enamel in their anterior teeth (for opening fruit with a hard husk); if this is true then the HSB in the posterior teeth may simply be a developmental consequence, such that a single genetic control mechanism for enamel decussation impacts all of the teeth in an animal's jaw. It is also possible that strong decussation may have an inverse relationship with enamel thickness: thin enamel and high decussation may provide the same crack-propagation inhibition as thick enamel with weaker decussation. Finally, well-developed HSB could be an unmodified ancestral character retained from a common hard-object feeding ancestor.

It is probably the combination of a seed's internal and external physical properties that provides the most important selective pressure for molar morphology. Most seeds masticated by *Pithecia* and *Chiropotes* have a pliable internal texture. Once the hard pericarp, together with the hard endocarp (if present), is removed with the anterior dentition, the material masticated by the molars has an even, elastic texture. The molar and premolar crenulations and reduced cusp relief in pitheciins may facilitate further breakdown of seed particles during crushing and grinding (terminal Phase I and Phase II chewing movements) (Lucas and Luke, 1984). These functions, rather than the puncture-crushing of the initial phase of mastication, may be the major function of the low relief of pitheciin molars. Crenulations may also aid in gripping seeds (holding them in place) that are soft and ductile, as opposed to hard and brittle (see also Lucas and Teaford (1994) for a discussion of the function of crenulations). Thin molar enamel is almost certainly the ancestral condition for platyrrhine primates, and the retention of thin molar enamel in the pitheciins is probably permitted by

the relative softness and nonabrasive properties of the masticated seeds.

Dietary differences between pitheciins and other platyrrhines appear to be related primarily to the physical properties of seeds in their diets, and how they process those seeds. Among non-pitheciin primates, only *Cebus* is an occasional seed-eater (in contrast to seed disperser). Significant aspects of *C. apella*'s adaptation to hard-object feeding (Kinzey, 1974) are its use of hands to open hard husks (Peres, 1991) and their thick-enameled molars to crush hard and brittle items, such as palm fruit, from which is obtained relatively hard mesocarp (for *Scheelea*) or the nut (for *Astrocarym*) (Janson and Boinski, 1992). The molars thus are occasionally subject to high stress during the initial puncture-crushing of these foods, and to abrasion as the hard, brittle food particles are further broken down during chewing. Thick enamel in *C. apella* consists of both an outer layer of radial prisms, a configuration that resists abrasive wear during chewing (Maas, 1993; Teaford et al., 1996; Maas and Dumont, 1999), and an inner layer of strong prism decussation, which resists crack propagation. The complex, thick molar enamel of *C. apella* appears to have evolved as an adaptation to both puncture-crushing and chewing hard, brittle foods. As noted above, while pitheciins use their strong anterior dentition to open the hard pericarp, the seeds that they puncture-crush and chew with their cheek teeth are tough but softer and more ductile. Presumably, the absence of a thick layer of radial enamel and the presence of strong HSB in pitheciin molars indicates that their teeth, though subject to normal chewing stress, are not subject to a high degree of abrasion. Kinzey and Norconk (1990) outlined the gross morphological features of the pitheciin sclerocarpic foraging adaptation. To these, we can add the combination of thin but strongly decussating molar enamel.

Identification of sclerocarpic foraging in fossil taxa

Kay (1981) demonstrated that terrestriality and an open country environment are not prerequisites for thick enamel in primates (*contra* Jolly, 1970). The present study further demonstrates that seed,

nut, and hard-fruit consumption do not predicate the evolution of thick molar enamel. Our results suggest that dietary reconstructions of fossil primates must consider the entire suite of evidence available, including concomitant adaptations of the anterior dentition and enamel microstructure, as well as enamel thickness.

The fossil hominoid *Kenyapithecus* has been portrayed as a sclerocarpic forager based on comparisons of its gnathic and dental anatomy with that of the pitheciins (McCrossin and Benefit, 1997: Table 1; Palmer et al., 1999). Analogous features of the pitheciin and *Kenyapithecus* masticatory systems include characters of the anterior dentition (heteromorphic incisors and splayed, robust canines), the mandible (robust corpus, well-developed inferior transverse torus), the posterior dentition (low cusps with crenulated molar enamel), and similar incisor microwear. In contrast to the thin molar enamel of the pitheciins, thick enamel has been inferred for *Kenyapithecus* based on radiographs and broken sections (Andrews and Martin, 1991). Our examination of a prepared thin-section of a lower left third premolar from Maboko Island (M36370) indicates that enamel decussation is well developed in *Kenyapithecus*, with HSB that have clear boundaries and extend nearly to the enamel surface (approximating the pitheciin condition). It must be noted, however, that the plane of section in M36370 is different from the plane of section used for the pitheciin molars in this study, and the tooth examined was a premolar rather than a molar. However, studies of a variety of extant primates (e.g., Maas, 1986, 1993, 1994) indicate that neither of these factors is likely to influence the appearance or distribution of prism decussation.

In order to assess the claim that *Kenyapithecus* was a sclerocarpic forager, it is necessary to consider the morphological evidence for sclerocarpic attributable to *Kenyapithecus* within the phylogenetic context of other Miocene hominoids. Unfortunately, the relationships of *Kenyapithecus* to other Miocene apes remain uncertain (e.g., Ward et al., 1999). If molar enamel in *Kenyapithecus* is relatively thick, as preliminary observations indicate, it suggests that, like *Cebus*, they used their molars to crush hard and abrasive

objects, rather than the softer, pliable seeds like those processed by the thin-enameled molars of the pitheciins. Thus, unlike the pitheciin primates, in *Kenyapithecus* both the anterior and posterior dentition was adapted to the dissipation of high forces induced by processing hard and abrasive foods. This combination of features of the anterior and posterior dentition is reminiscent of the hominoids *Griphopithecus*, *Sivapithecus*, and *Afropithecus*, all of which have stout, heteromorphic incisors and relatively thick molar enamel (Martin, 1983, 1985; Andrews and Martin, 1991). The canines of *Sivapithecus* and *Afropithecus* also are robust and laterally splayed, as in *Kenyapithecus* and the pitheciins (Leakey and Leakey, 1986; Ward and Pilbeam, 1983). The anatomy of *Kenyapithecus* thus appears to be consistent with that of other middle Miocene hominoids from Africa, Asia, and Europe, rather than uniquely similar to the pitheciins. Analysis of the incisor microwear of these and other Miocene hominoids may shed light on whether only *Kenyapithecus*, or middle Miocene apes in general, were sclerocarpic foragers. The relatively thick molar enamel of *Kenyapithecus* and other middle Miocene hominoids indicates that they masticated hard and/or abrasive objects with their molars, unlike pitheciins, although they would also likely have been able to break into tough pericarp and process the seeds.

Conclusions

This study of molar enamel thickness in platyrrhines demonstrates that the pitheciin primates (the saki-uakaris: *Cacajao*, *Chiropotes*, *Pithecia*) have a surprising combination of thin molar enamel and strong prism decussation (i.e., narrow, well-defined HSB that extend throughout the thickness of the enamel). Their thin enamel is unexpected because hard fruits constitute a large percentage of the pitheciin diet. With the exception of the thick-enameled molars of the hard-object feeder *Cebus apella*, which also has less extensive prism decussation than do the pitheciins, all of the other platyrrhines examined have thin enamel and less extensive or no enamel decussation.

Thick enamel is not a prerequisite for tough object feeding. Although both the pitheciins and *C. apella* include hard foods in their diets, only the latter has thick-enameled cheek teeth. In the case of *C. apella*, thick molar enamel consisting of a substantial outer layer of radial prisms coupled with an inner layer of well-defined HSB serves to prolong the life of a tooth that is subjected to both abrasion and high chewing stresses induced by the mastication of hard and brittle objects. In contrast, the pitheciins use their anterior dentition to break down hard food objects, while their thin-enameled molars, with enamel microstructure that is not well designed to resist abrasive wear, appear to be used to chew more pliable objects.

The presence of HSB in pitheciin molars can be explained by body size alone. However, the very strong development of the HSB, coupled with the absence of an appreciable outer layer of abrasion-resistant, radially-oriented prisms and very thin enamel, appears, thus far, to be unique among living primates (Maas and Dumont, 1999). While thin enamel is probably primitive for platyrrhines, the very strong decussation and thin layer of radial enamel is almost certainly derived. Moreover, as Martin (1983, 1985) has demonstrated for hominoids, thin enamel in one taxon may differ, developmentally and evolutionarily, from thin enamel in another.

Based on similarities of its gnathic and dental morphology to the pitheciins, the fossil hominoid *Kenyapithecus* has been described as a sclerocarpic forager. However, the thick molar enamel in *Kenyapithecus*, which implies that it masticated relatively hard or abrasive food with its molars, argues against a dietary repertoire similar to that of the pitheciins. Many of the traits shared between the pitheciins and *Kenyapithecus* also appear in other middle Miocene hominoids; uncertainty surrounding the phylogenetic relationships and even which fossils are attributable to the genus *Kenyapithecus* (and other Miocene genera) make it difficult to assess the polarity of this suite of characters. When interpreting the dietary regime of a fossil species, morphological aspects of anterior and posterior dental morphology, enamel microstructure, and phylogenetic relationships should all be taken into consideration.

Acknowledgements

Specimens for this study were graciously loaned by the Department of Mammalogy, Smithsonian Institution National Museum of Natural History; the Department of Anatomical Sciences at Stony Brook University; the American Museum of Natural History (New York); and the British Museum of Natural History (London). Don Reid provided

unpublished measurements of *Tupaia tana* enamel thickness. We thank D. Boyer, J. Lodwick, T. Smith, and L. Ulhaas for comments and discussion on earlier drafts of this manuscript. Comments from W. Kimbel, M. Teaford, and two anonymous reviewers greatly improved this manuscript. This research was partially supported by NSF grant SBR 8918695.

Appendix A.

Taxon	Tooth	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
<i>Aotus trivergatus</i>	M ¹	0.18	0.29	0.16	0.22	0.16	0.16	0.18	0.16	0.25	0.72	0.73	0.30	0.20	2.97
<i>Aotus trivergatus</i>	M ²	0.29	0.38	0.20	0.21	0.14	0.19	0.27	0.19	0.33	0.49	0.50	0.39	0.29	3.14
<i>Aotus trivergatus</i>	M ₁	0.31	0.34	0.26	0.25	0.24	0.23	0.18	0.40	0.17	0.24	0.22	0.38	0.33	1.85
<i>Ateles paniscus</i>	M ²	0.20	0.24	0.26	0.29	0.23	0.27	0.30	0.27	0.27	1.39	1.39	0.26	0.22	5.09
<i>Ateles paniscus</i>	M ³	0.24	0.25	0.18	0.18	0.17	0.15	0.25	0.17	0.23	0.53	0.52	0.28	0.35	3.91
<i>Ateles paniscus</i>	M ³	0.33	0.31	0.24	0.26	0.19	0.28	0.28	0.26	0.30	1.10	1.08	0.31	0.33	4.24
<i>Ateles paniscus</i>	M ¹	0.15	0.15	0.22	0.19	0.21	0.34	0.31	0.33	0.33	1.51	1.51	0.14	0.15	4.68
<i>Cacajao calvus</i>	M ²	0.32	0.44	0.26	0.37	0.21	0.42	0.42	0.44	0.56	0.55	0.56	0.46	0.38	3.64
<i>Cacajao calvus</i>	M ₂	0.21	0.36	0.31	0.30	0.28	0.36	0.27	0.52	0.28	0.55	0.55	0.36	0.21	3.22
<i>Cacajao calvus</i>	M ₃	0.33	0.35	0.29	0.34	0.25	0.28	0.40	0.29	0.41	0.25	0.25	0.38	0.33	2.77
<i>Callicebus moloch</i>	M ₂	0.48	0.24	0.57	0.33	0.33	0.32	0.24	0.38	0.24	0.39	0.38	0.24	0.49	2.15
<i>Cebus apella</i>	M ₁	0.67	0.61	0.67	0.44	0.29	0.61	0.46	0.73	0.45	0.62	0.63	0.61	0.66	3.34
<i>Cebus apella</i>	M ₂	0.59	0.58	0.59	0.54	0.52	0.62	0.41	0.67	0.40	0.51	0.51	0.59	0.59	3.03
<i>Chiropotes satanas</i>	M ²	0.31	0.30	0.30	0.30	0.22	0.24	0.35	0.26	0.38	0.37	0.39	0.30	0.30	3.75
<i>Chiropotes satanas</i>	M ₂	0.23	0.31	0.34	0.21	0.22	0.32	0.19	0.34	0.20	0.37	0.37	0.31	0.24	2.52
<i>Chiropotes satanas</i>	M ₂	0.15	0.34	0.19	0.20	0.20	0.36	0.21	0.37	0.23	0.38	0.40	0.35	0.15	2.64
<i>Pithecia monachus</i>	M ¹	0.25	0.28	0.28	0.32	0.22	0.29	0.31	0.30	0.35	0.62	0.62	0.29	0.26	3.96
<i>Pithecia monachus</i>	M ₁	0.43	0.36	0.34	0.39	0.29	0.27	0.21	0.27	0.23	0.49	0.48	0.38	0.44	3.24

Measurements defined in Martin (1983).

Appendix B. Enamel thickness values of primates and other mammals

Taxon	n	RET	Source
Primates			
Cercopithecoidea			
<i>Cercocebus albigena</i>	2	16.85	Dumont (1995)
<i>Cercocebus torquatus</i>	3	12.89	Dumont (1995)
<i>Cercopithecus mona</i>	1	11.29	Shellis et al. (1998)
<i>Cercopithecus</i> sp.	1	13.83	Shellis et al. (1998)
<i>Cercopithecus</i> spp.	32	13.92	Ulhaas et al. (1999)
<i>Colobus</i> spp.	23	12.31	Ulhaas et al. (1999)
<i>Eurythrocebus patas</i>	2	12.31	Shellis et al. (1998)
<i>Macaca arctoides</i>	1	12.82	Shellis et al. (1998)
<i>Macaca mulatta</i>	4	13.30	Shellis et al. (1998)
<i>Macaca nemestrina</i>	3	14.24	Shellis et al. (1998)
<i>Papio cynocephalus</i>	4	16.11	Shellis et al. (1998)
<i>Presbytis cristatus</i>	2	11.68	Shellis et al. (1998)
<i>Theropithecus gelada</i>	10	15.51	Shellis et al. (1998); Swindler and Beynon (1993)

Appendix B. (continued)

Taxon	n	RET	Source
Hominoidea			
<i>Gorilla gorilla</i>	27	9.66	Martin (1983); Shellis et al. (1998)
<i>Homo sapiens</i>	65	20.09	Martin (1983); Shellis et al. (1998)
<i>Hylobates</i> sp.	1	11.09	Martin (1983); Shellis et al. (1998)
<i>Pan paniscus</i>	1	14.00	Smith et al. (2003)
<i>Pan troglodytes</i>	22	11.60	Martin (1983); Shellis et al. (1998)
<i>Pongo pygmaeus</i>	24	15.33	Martin (1983); Shellis et al. (1998)
Ceboidea			
<i>Alouatta villosa</i>	2	10.88	Shellis et al. (1998)
<i>Aotus trivergatus</i>	3	11.73	This Study
<i>Ateles paniscus</i>	4	8.89	This Study
<i>Ateles</i> sp.	1	13.07	Shellis et al. (1998)
<i>Cacajao calvus</i>	3	11.54	This Study
<i>Callicebus moloch</i>	1	12.32	This Study
<i>Callithrix jacchus</i>	3	8.29	Shellis et al. (1998)
<i>Cebus apella</i>	4	19.57	Dumont (1995); Shellis et al. (1998); This Study
<i>Cebus capucinus</i>	3	15.13	Dumont (1995)
<i>Chiropotes satanas</i>	3	9.54	This Study
<i>Pithecia monachus</i>	2	11.61	This Study
<i>Saimiri sciureus</i>	5	8.73	Shellis et al. (1998)
Lemuroidea			
<i>Daubentonia madagascarensis</i>	1	21.68	Shellis et al. (1998)
<i>Lemur catta</i>	1	8.10	Shellis et al. (1998)
<i>Lemur</i> sp.	2	6.99	Shellis et al. (1998)
<i>Propithecus diadema</i>	2	9.26	Shellis et al. (1998)
<i>Propithecus verreauxi</i>	1	8.26	Shellis et al. (1998)
<i>Varecia variegata</i>	1	5.68	Shellis et al. (1998)
Lorisoidea			
<i>Galago</i> sp.	1	5.74	Shellis et al. (1998)
<i>Nycticebus coucang</i>	5	10.46	Shellis et al. (1998)
<i>Otolemur crassicaudatus</i>	1	5.63	Shellis et al. (1998)
<i>Otolemur garnetti</i>	1	9.26	Shellis et al. (1998)
<i>Perodicticus potto</i>	3	7.93	Shellis et al. (1998)
Tarsioidea			
<i>Tarsius</i> sp.	1	8.45	Shellis et al. (1998)
Chiroptera			
Vespertilionoidea			
<i>Eumops perotis</i>	2	3.24	Dumont (1995)
<i>Eumops underwoodi</i>	3	3.91	Dumont (1995)
Rhinolophoidea			
<i>Hipposideros caffer</i>	3	3.99	Dumont (1995)
<i>Hipposideros commersoni</i>	5	5.47	Dumont (1995)
Vespertilionoidae			
<i>Myotis lucifugus</i>	4	4.60	Dumont (1995)
<i>Myotis velifer</i>	3	5.14	Dumont (1995)
Scandentia			
Tupaioidea			
<i>Tupaia tana</i>	1	8.42	Don Reid (Personal Communication)

RET is the weighted average of all of the molars measured in each of the studies listed.

References

- Anapol, F., Lee, S., 1994. Morphological adaptation to diet in platyrrhine primates. *Am. J. Phys. Anthropol.* 94, 239–261.
- Andrews, P., Martin, L.B., 1991. Hominoid dietary evolution. *Phil. Trans. R. Soc. Lond. B* 334, 199–209.
- Ayres, J.M., 1986. Uakaris and Amazonian flooded forest. Ph.D. Dissertation, University of Cambridge.
- Ayres, J.M., 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J. Hum. Evol.* 18, 697–716.
- Barnett, A., da Cunha, A.C., 1991. The golden-backed uakari on the upper Rio Negro, Brazil. *Oryx* 25, 80–88.
- Boubli, J.P., 1999. Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico da Neblina National Park, Brazil. *Int. J. Primatol.* 20, 719–749.
- Boubli, J.P., Ditchfield, A.D., 2000. The time of divergence between the two species of uakari monkeys: *Cacajao calvus* and *Cacajao melanocephalus*. *Folia Primatol.* 71, 387–391.
- Boyde, A., Tamarin, A., 1984. Improvement to critical point drying technique for SEM. *Scanning* 6, 30–35.
- Dumont, E.R., 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. *J. Mammal.* 76, 1127–1136.
- Grine, F.E., Martin, L., 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine, F.E. (Ed.), *Evolutionary History of the “Robust” Australopithecines*, pp. 3–42.
- Hershkovitz, P., 1985. A preliminary taxonomic review of the South American bearded saki monkeys, genus *Chiropotes* (Cebidae, Platyrrhini), with the description of a new form. *Fieldiana Zoology* 27, 1–46.
- Janson, C.H., Boinski, S., 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. *Am. J. Phys. Anthropol.* 88, 483–498.
- Janzen, D.H., 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2, 465–492.
- Jolly, C.J., 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5, 5–26.
- Kay, R.F., 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthropol.* 55, 141–151.
- Kay, R.F., Johnson, D., Meldrum, D.J., 1998. A new pitheciin primate from the middle Miocene of Argentina. *Am. J. Primatol.* 45, 317–336.
- Kinzey, W.G., 1974. Ceboid models for the evolution of hominoid dentition. *J. hum. Evol.* 3, 193–203.
- Kinzey, W.G., 1992. Dietary and dental adaptations in the Pitheciinae. *Am. J. Phys. Anthropol.* 88, 499–514.
- Kinzey, W.G., Norconk, M.A., 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am. J. Phys. Anthropol.* 81, 5–15.
- Kinzey, W.G., Norconk, M.A., 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int. J. Primatol.* 14, 207–227.
- Leakey, R.E.F., Leakey, M.G., 1986. A new Miocene hominoid from Kenya. *Nature* 324, 143–146.
- Lehman, S.M., Robertson, K.L., 1994. Preliminary survey of *Cacajao melanocephalus melanocephalus* in southern Venezuela. *Int. J. Primatol.* 15, 927–934.
- Lucas, P.W., Luke, D.A., 1984. Chewing it over: basic principles of food breakdown. In: Chivers, D.J., Wood, B.A., Bilsborough, A. (Eds.), *Food Acquisition and Processing in Primates*. Plenum Press, New York, pp. 283–301.
- Lucas, P.W., Teaford, M., 1994. Functional morphology of colobine teeth. In: Davies, A.G., Oates, J.F. (Eds.), *Colobine Monkeys: Their Ecology, Behavior, and Evolution*. Cambridge University Press, Cambridge, pp. 173–204.
- Maas, M.C., 1986. Function and variation of enamel prism decussation in ceboid primates. *Am. J. Phys. Anthropol.* 69, 233–234.
- Maas, M.C., 1993. Enamel microstructure and molar wear in the greater galago, *Otolemur crassicaudatus* (Mammalia, Primates). *Am. J. Phys. Anthropol.* 92, 217–233.
- Maas, M.C., 1994. Enamel microstructure in Lemuridae (Mammalia, Primates)—assessment of variability. *Am. J. Phys. Anthropol.* 95, 221–241.
- Maas, M.C., Dumont, E.R., 1999. Built to last: the structure, function, and evolution of primate dental enamel. *Evol. Anthropol.* 8, 133–152.
- Macho, G.A., Berner, M.E., 1993. Enamel thickness of human maxillary molars reconsidered. *Am. J. Phys. Anthropol.* 92, 189–200.
- Macho, G.A., Berner, M.E., 1994. Enamel thickness and the helocoidal occlusal plane. *Am. J. Phys. Anthropol.* 94, 327–337.
- Martin, L.B., 1983. The relationships of the later Miocene Hominoidea. Ph.D. Dissertation, University College London.
- Martin, L.B., 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314, 260–263.
- Martin, L.B., Boyde, A., Grine, F.E., 1988. Enamel structure in primates—a review of scanning electron-microscope studies. *Scanning Microsc.* 2, 1503–1526.
- McCrossin, M.L., Benefit, B.R., 1997. On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the middle Miocene of eastern Africa. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 241–267.
- Meldrum, D.J., Kay, R.F., 1997. *Nuciraptor rubricae*, a new pitheciin seed predator from the Miocene of Colombia. *Am. J. Phys. Anthropol.* 102, 407–427.
- Norconk, M.A., Grafton, B.W., Conklin-Brittain, N.L., 1998. Seed dispersal by neotropical seed predators. *Am. J. Primatol.* 45, 103–126.
- Orlosky, F.J., 1973. Comparative dental morphology of extant and extinct Cebidae. Ph.D. Dissertation, University of Washington.
- Palmer, A.K., Benefit, B.R., McCrossin, M.L., 1999. Was *Kenyapithecus africanus* a sclerocarpic feeder? *An*

- exploration of the dietary adaptations of a middle Miocene hominoid through anterior dental microwear analysis. *Am. J. Phys. Anthropol.* 108, 217.
- Peres, C.A., 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23, 262–270.
- Pfretzschner, H.U., 1986. Structural reinforcement and crack propagation in enamel. In: Russell, D.E., Santoro, J.P., Sigoneau-Russell, D. (Eds.), *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology*, Paris, 1986. *Mem. Mus. Nat. Hist. Nat. Paris (ser. C)*, Paris, pp. 133–143.
- Rensberger, J.M., 1993. Adaptation of enamel microstructure to differences in stress intensity in the Eocene perissodactyl *Hyracotherium*. In: Kobayashi, I., Mutvei, H., Sahni, A. (Eds.), *Structure, Formation, and Evolution of Fossil Hard Tissues*. Tokai University Press, Tokyo, pp. 131–145.
- Rosenberger, A.L., 1979. Phylogeny, evolution, and classification of New World Monkeys (Platyrrhini, Primates). Ph.D. Dissertation, City University of New York.
- Rosenberger, A.L., Kinzey, W.G., 1976. Functional patterns of molar occlusion in platyrrhine primates. *Am. J. Phys. Anthropol.* 45, 281–298.
- Schwartz, G.T., 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am. J. Phys. Anthropol.* 111, 221–244.
- Shellis, R.P., Beynon, A.D., Reid, D.J., Hiiemae, K.M., 1998. Variation in molar enamel thickness among primates. *J. Hum. Evol.* 35, 507–522.
- Smith, T.M., Martin, L.B., Leakey, M.G., 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J. hum. Evol.* 44, 283–306.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed, W.H. Freeman and Company, New York.
- Swindler, D.R., 1976. *Dentition of Living Primates*. Academic Press, London.
- Swindler, D.R., Beynon, A.D., 1993. The development and microstructure of the dentition of *Theropithecus*. In: Jablonski, N.G. (Ed.), *Theropithecus: the Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 351–381.
- Teaford, M.F., Maas, M.C., Simons, E.L., 1996. Dental microwear and microstructure of early Oligocene primates from the Fayum, Egypt: implications for diet. *Am. J. Phys. Anthropol.* 101, 527–544.
- Ulhaas, L., Henke, W., Rothe, H., 1999. Variation in molar enamel thickness of the genera *Cercopithecus* and *Colobus*. *Anthropologie* 37, 265–271.
- van Roosmalen, M.G.M., Mittermeier, R.A., Fleagle, J.G., 1988. Diet of the northern bearded saki (*Chiropotes satanas*): a neotropical seed predator. *Am. J. Primatol.* 14, 11–35.
- von Koenigswald, W., Clemens, W.A., 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scanning Microscopy* 6, 195–218.
- von Koenigswald, W., Rensberger, J.M., Pfretzschner, H.U., 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* 328, 150–152.
- Ward, S., Brown, B., Hill, A., Kelley, J., Downs, W., 1999. *Equatorius*: a new hominoid genus from the middle Miocene of Kenya. *Science* 285, 1382–1386.
- Ward, S.C., Pilbeam, D.R., 1983. Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In: Ciochon, R.L., Corruccini, R.S. (Eds.), *New Interpretations of Ape and Human Ancestry*. Plenum Press, New York, pp. 211–238.